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SHORT COMMUNICATION

ALBULIFORM FISH REMAINS (TELEOSTEI, ELOPOMORPHA) FROM THE LOWER CRETACEOUS (VALANGINIAN) WADHURST CLAY FORMATION OF THE WEALDEN SUPERGROUP OF SOUTHEAST ENGLAND

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Fish remains are abundant in many strata of the Lower Cretaceous (Berriasian–early Aptian) Wealden Supergroup of southern England (Fig. 1A). They are particularly abundant in the ‘bone beds’ of the Weald Sub-basin of mainland Britain (Allen, 1949; Cook, 1995) and at numerous horizons in the Wessex Sub-basin, especially the plant debris beds (Sweetman and Insole, 2010) of the Wessex Formation (Wealden Group) of the Isle of Wight. However, with the exception of a study documenting the first record of a neoselachian from the freshwater, Barremian, Wessex Formation of the Isle of Wight (Sweetman and Underwood, 2006) and recent brief reviews of the chondrichthyan (Duffin and Sweetman, 2011) and osteichthyan (Forey and Sweetman, 2011) assemblages, the fishes of the Wealden Supergroup have received scant attention since Woodward’s early 20th century monograph (Woodward, 1916–1919) and Patterson’s (1966) reevaluation of Wealden sharks.

Articulated remains are uncommon but complete skulls of the shark *Egertonodus* have been recorded from mainland Britain (Maisey, 1983) and from the Isle of Wight. Occasionally articulated remains of the lepisosteiform *Scheenstia mantelli* López-Arbarello, 2012 (until recently placed in the genus *Lepidotes* Agassiz, 1832, and considered to be a semionotiform), have been found at various localities in southeast England (e.g., Forey and Sweetman, 2011:230, text-fig. 18.3A) and on the Isle of Wight, and articulated remains of leptolepid fishes (Ross and Cook, 1995) and a death assemblage of articulated fishes, including a pycnodont, have been recorded at Smokejacks Brickworks, Ockley, Surrey (Forey and Sweetman, 2011). However, as demonstrated by Sweetman and Underwood (2006), the recovery and study of microvertebrate remains holds the potential to shed valuable new light on the fishes of the Wealden Supergroup. To date, work on the large number of microvertebrate remains recovered from the Wessex Formation of the Isle of Wight has concentrated on the tetrapods (for a summary, see Martill et al., 2011; Sweetman, 2011; Sweetman and Evans, 2011a, 2011b; Sweetman and Hooker, 2011). On the mainland, no sustained search for microvertebrate remains has been undertaken since that directed by the late Kenneth Kermack in the 1960s and 1970s (e.g., Clemens and Lees, 1971). However, in recent years, samples from Ashdown Brickworks near Bexhill, East Sussex (Fig. 1B), were taken from a number of horizons (Fig. 2) and processed using bulk screening techniques for the recovery of microvertebrate remains. Those from a bone bed known locally as the ‘conglomerate bed’ (Fig. 2) were found to be the most productive and have yielded numerous isolated teeth of an albuliform fish, representing to date the earliest record of this clade. Teeth of albuliforms are distinct from those of other durophagous Early Cretaceous freshwater taxa, e.g., pycnodontiforms, tritoral lepisosteiforms and semionotiforms, and some hybodontiforms, on the basis of four characteristics, which are further described below: the presence of a basal acrodin-covered ring surrounding the area of attachment to an underlying stack of replacement teeth seen only in some members of the Phyllodontidae Dartevelle and Casier, 1943; their apicobasal

compression; their variably irregular subcircular to suboval outline in apical and basal views; and the rugose or pustulate apical ornamentation of unworn specimens (Estes, 1969).

Institutional Abbreviation—BEXHM, Bexhill Museum, Bexhill, East Sussex, U.K.

GEOGRAPHIC, GEOLOGIC, AND PALEONTOLOGIC SETTINGS

Ashdown Brickworks is situated northwest of Bexhill, East Sussex (Fig. 1). It incorporates two pits exploiting argillaceous and arenaceous strata in the mid-Valanginian part (Gallois and Worssam, 1993) of the Hastings Group. Of these, Crowborough Pit has yet to yield vertebrate fossils, but a number of strata in the more northerly Pevensey Pit, which is in the upper part of the Wadhurst Clay Formation and the lowest part of the overlying Tunbridge Wells Sand Formation (Fig. 2), have yielded a diverse assemblage of aquatic and terrestrial vertebrates (Naish and Sweetman, 2011). The clay known locally as the ‘lower clay’ contains two bone bed horizons (Fig. 2) representing channel lags of variable lateral thickness and extent. All vertebrate remains in these deposits are polished or abraded to a greater or lesser extent as a result of transport processes in an aqueous environment but delicate structures such as the neural arches on salamander vertebrae are sometimes preserved (e.g., Sweetman and Evans, 2011a:text-fig. 20.4A–E). The bed known locally as the ‘conglomerate bed’ comprising the upper of the two bone beds is generally between 5 and 6 cm thick. It is the most palaeontologically diverse, yielding abundant bones, bone fragments, teeth, scales, and other isolated elements. These represent chondrichthyan and osteichthyan fishes, salamanders, frogs, aquatic and terrestrial lizards, turtles, crocodyliforms, pterosaurs, and dinosaurs (Naish and Sweetman, 2011). The lowermost of the bone beds is known locally as the ‘turtle bed’ (Fig. 3). As suggested by the name, it is rich in turtle remains but yields a less diverse vertebrate assemblage than the bed above. During the study in progress and excluding the albuliform, teeth of which are described below, the following chondrichthyan and actinopterygian taxa have been recorded:

CHONDRICHTHYES

Hybodontiformes

Hybodontidae

Polyacrodontidae

Polyacrodus brevicostatus

Hybodontidae

Egertonodus basanus

Planohybodus ensis

Polyacrodus parvidens

Lonchidiidae

Lonchidion breve

Lonchiodon sp.

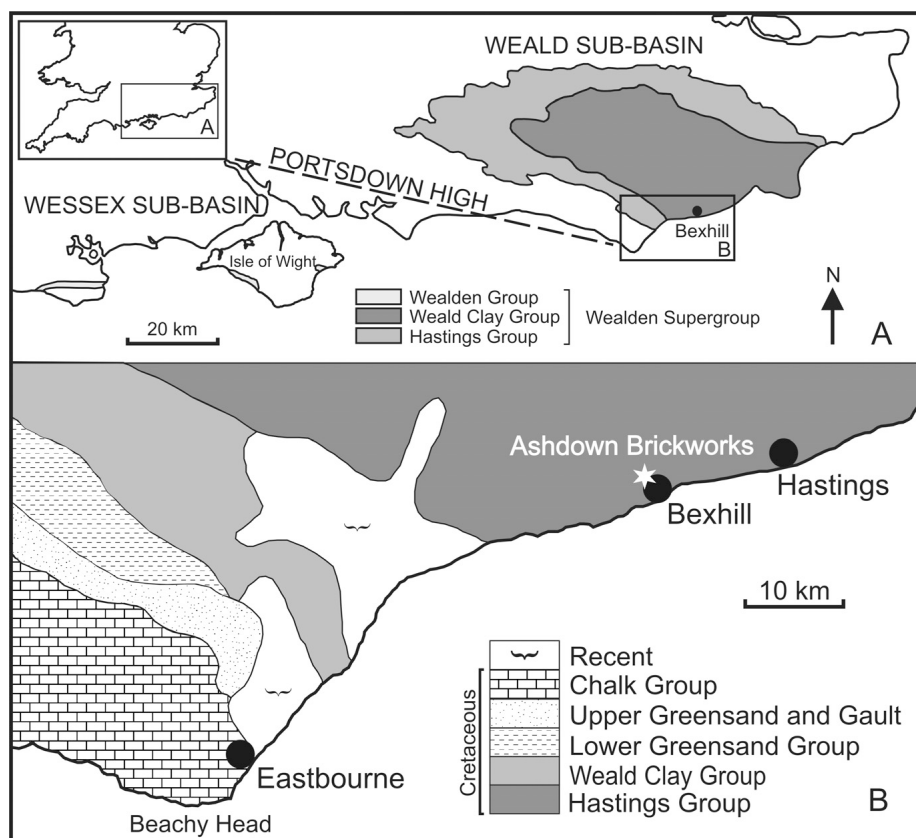


FIGURE 1. **A**, location and outline geological maps showing Wealden Supergroup outcrop areas in southeast England and the locations of the Weald and Wessex sub-basins; **B**, outline geological map of the area around Bexhill indicating the location of Ashdown Brickworks.

ACTINOPTERYGII

Pycnodontiformes

Coelodus sp.

Lepisosteiformes

Scheenstia mantelli

Amiiformes

Caturidae

Neorhombolepis sp.

Leptolepiformes

Pachythrissops sp.

SYSTEMATIC PALEONTOLOGY

Cohort ELOPOMORPHA sensu Greenwood, Rosen, Weitzman, and Myers, 1966

Order ALBULIFORMES sensu Forey, Littlewood, Richtie, and Myer, 1996

Suborder ALBULOIDEI sensu Forey, Littlewood, Richtie, and Myer, 1996

Family PHYLLODONTIDAE Dartevelle and Casier, 1943

?Subfamily PHYLLODONTINAE Dartevelle and Casier, 1949

?PHYLLODONTINAE indet.

(Fig. 3)

Material—Numerous isolated teeth represented by BEXHM:2012.21.1 (Fig. 3A–C), BEXHM:2012.21.2 (Fig. 3D, E), BEXHM:2012.21.3 (Fig. 3F, G), BEXHM:2012.21.4 (Fig. 3H, I), BEXHM:2012.21.5 (Fig. 3J, K), BEXHM:2012.21.6 (Fig. 3L, M), and BEXHM:2012.21.7 (Fig. 3N, O); BEXHM:2012.21.8 (Fig. 3P) and BEXHM:2012.21.9 (Fig. 3Q), two worn teeth broken in half to reveal acrodin and orthodentine structure in cross-section; and BEXHM:2012.21.10 (Fig. 3R), a tooth to which is attached a somewhat abraded replacement tooth; also

BEXHM:2012.21.11 (not figured), a collection of seven teeth further documenting tooth replacement; BEXHM:2012.21.12 (not figured), a collection of 25 teeth documenting further variation in size and crown morphology.

Horizon and Locality—Currently known only from a bone bed locally named the ‘conglomerate bed’ occurring approximately 27.6 m below the top of the Wadhurst Clay Formation (Fig. 2) exposed in the Pevensy Pit at Ashdown Brickworks, Bexhill, East Sussex, U.K. (Fig. 1B). Samples processed for microvertebrate remains and yielding the accessioned specimens were taken at and close to British National Grid Reference TQ 71940 09624.

DESCRIPTION

Teeth are generally subcircular or suboval in occlusal and basal outlines, but some are slightly kidney-shaped (Fig. 3). They are apicobasally flattened with a convex occlusal surface (Fig. 3C). Most of the teeth have smooth occlusal surfaces as a result of dietary attrition from trituration and/or abrasion during transport. Tooth crowns are variably rugose when unworn (Fig. 3H, J, L, N) and in some the rugosity is rather coarse. Tooth diameter ranges from 0.8 to 5.9 mm, but most are between 2 and 3 mm. The area of attachment lacks a pulp cavity and in unworn specimens is variably rugose and/or pitted (e.g., Fig. 3G; cf. Fig. 3B). It is also surrounded by a basally convex, acrodin-covered ring, the acrodin being an extension of that occurring on the occlusal surface (Fig. 3B, C, E, G). In specimens with an unworn, rugose, occlusal surface, rugosity also extends to the basal ring (Fig. 3K, M). In abraded and broken specimens, crowns can be seen to consist of a variable number of basal layers of orthodentine. In some specimens, these layers are of variable thickness and appear to be sharply folded (Fig. 3P). In others, folding is largely absent or of low amplitude, orthodentine layers are more equal in thickness and follow the occlusal profile of the

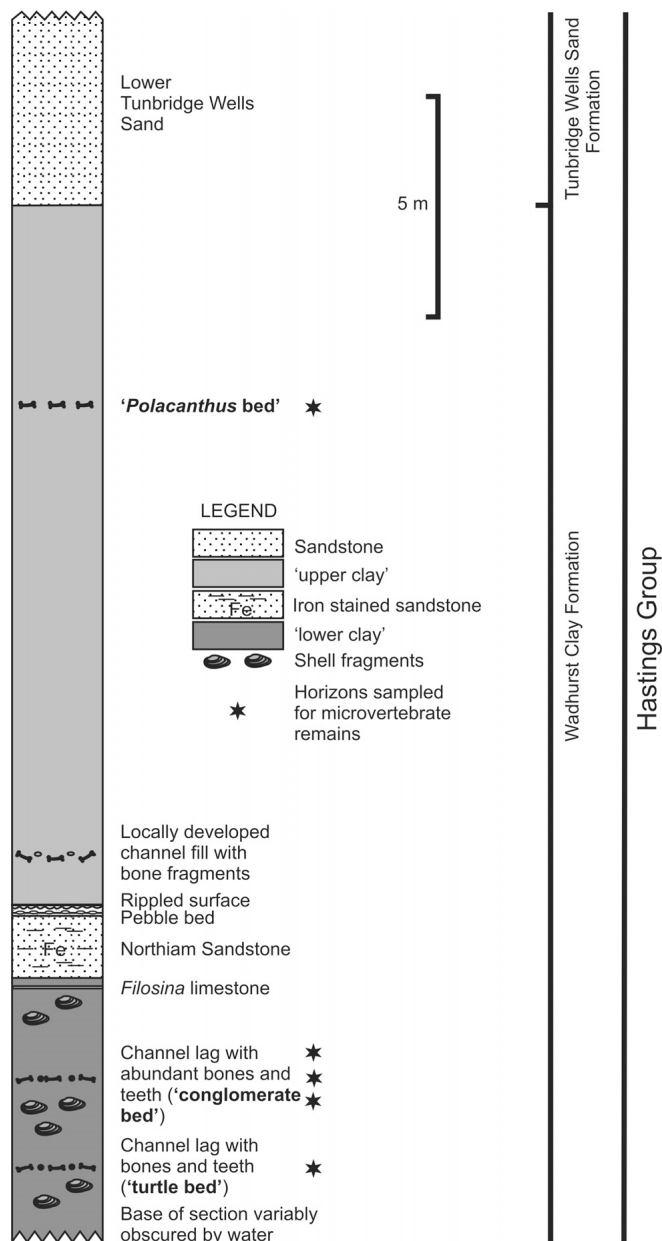


FIGURE 2. Schematic lithological log of the Hastings Group exposed at Pevensey Pit, Ashdown Brickworks, based on field data collected in February 2010.

tooth (Fig. 3Q). A thin layer of acrodin, usually approximately equal in thickness to individual orthodontine layers below, covers the crown. In the specimen shown in Figure 3P, the acrodin incorporates numerous very fine, apicobasally orientated tubules, as typically observed in this type of tooth tissue. Medullary canals and orthodontinal tubules appear to be absent, but a histological study of thin sections, beyond the scope of this short communication, is required to confirm this. A small number of specimens including BEXHM:2012.21.10 (Fig. 3R) and those constituting BEXHM:2012.21.11 (not figured) document the tooth replacement pattern of the Ashdown albuliform. Although all specimens are abraded to a greater or lesser extent and only one comprises more than two teeth (a heavily abraded specimen forming part of BEXHM:2012.21.11), in all, replacement teeth are stacked directly below functional teeth.

The Ashdown specimens can be unequivocally identified as teeth, even though isolated, worn specimens are superficially similar in gross morphology to crayfish gastroliths (Scott and Duncan 1967; Wings, 2007) that have been recorded from some Late Cretaceous sites in North America and confused with the teeth of albuliform fishes (D. Brinkman, pers. comm., 2012). Furthermore, although crayfish have been recorded from the Wealden Supergroup of mainland Britain (Jarzembowski, 2011), they are extremely rare. Crayfish gastroliths mostly comprise calcium carbonate and effervesce in 5% hydrochloric acid. No chemical analysis of the Ashdown specimens has been undertaken, but they do not effervesce in dilute HCl. Also, when broken in half, broken surfaces below the acrodin layer are conchoidal and vitreous, closely resembling the orthodontine seen in broken teeth of other taxa. A single crayfish gastrolith has recently been recovered from the Hauterivian Lower Weald Clay Formation of the Wealden Supergroup exposed at Keymer Tileworks, Burges Hill, West Sussex (S.C.S., work in progress), but they have not been recorded at Ashdown Brickworks. At this locality, teeth of the sort described above are abundant, albeit and pending further sampling, apparently at only one horizon.

DISCUSSION AND CONCLUSIONS

Among fossil albuliform taxa, including those based on otoliths occurring in the Albian Gault Clay Formation of southern Britain (Stinton, 1973), most have been recorded from fully marine, estuarine, and saline lagoonal settings. Exceptions are taxa from the uppermost Cretaceous, brackish, coastal deltaic deposits of Quintanilla la Ojada, Burgos, Spain (Berreteaga et al., 2011), from the ?Aptian Santana Formation of Brazil (Mayrinck et al., 2010, and references therein), and from the Aptian Dongmyeong Formation of Korea (Imaoka et al., 1993; Yabumoto et al., 2006). The Santana Formation is a mainly fluvial, deltaic, and lagoonal-lacustrine succession with occasional brief marine incursions from either the Central or South Atlantic oceans (Berthou, 1990; Martill and Wilby, 1993). The Dongmyeong Formation represents deposition in freshwater. However, based on comparisons with extant taxa and the occurrence of well-preserved, articulated, albuliform specimens representing individuals recently metamorphosed from leptocephali, Yabumoto et al. (2006) conclude that the Dongmyeong Formation was probably deposited in a near-coast setting with connections to the sea. The Wadhurst Clay Formation is interpreted as having been deposited primarily in lacustrine settings, with ostracods, spinicaudatans, and molluscs indicating freshwater to slightly saline environments. Isotope data (Allen et al., 1973) also provide support for minor fluctuations in salinity, suggesting occasional connection of the lake system to saline waters of either the Boreal or, less certainly, the Tethyan Realm (Allen, 1981). However, based on Allen's paleogeographical reconstruction (1981:390, fig. 8), the site yielding the specimens described here was at least 100 and perhaps as much as 200 km from the nearest coastline and at the distal extremity of any marine influence. Furthermore, all other taxa recovered from the 'conglomerate bed' at Ashdown Brickworks are derived from freshwater or terrestrial environments (Batten, 2011, and references therein). This would suggest that the Wadhurst Clay Formation albuliform remains represent a taxon (or taxa, see below) that was resident in freshwater, and not diadromous as are the extant, western Atlantic, omnivorous, demersal *Albula nernoptera* and the Indo-Pacific, carnivorous, reef-associated *A. neoguinaica* (data from Froese and Pauly, 2012). However, isotopic analyses are required to confirm this.

The mid-Valanginian, Wealden albuliform remains represent, to date, the earliest record of this clade; the previous oldest record being *Baugeichthys caeruleus* Filleul, 2000, from, at earliest, the late Hauterivian and possibly later Early Cretaceous (Clavel et al., 2007) of the Massif des Bauges, France. They

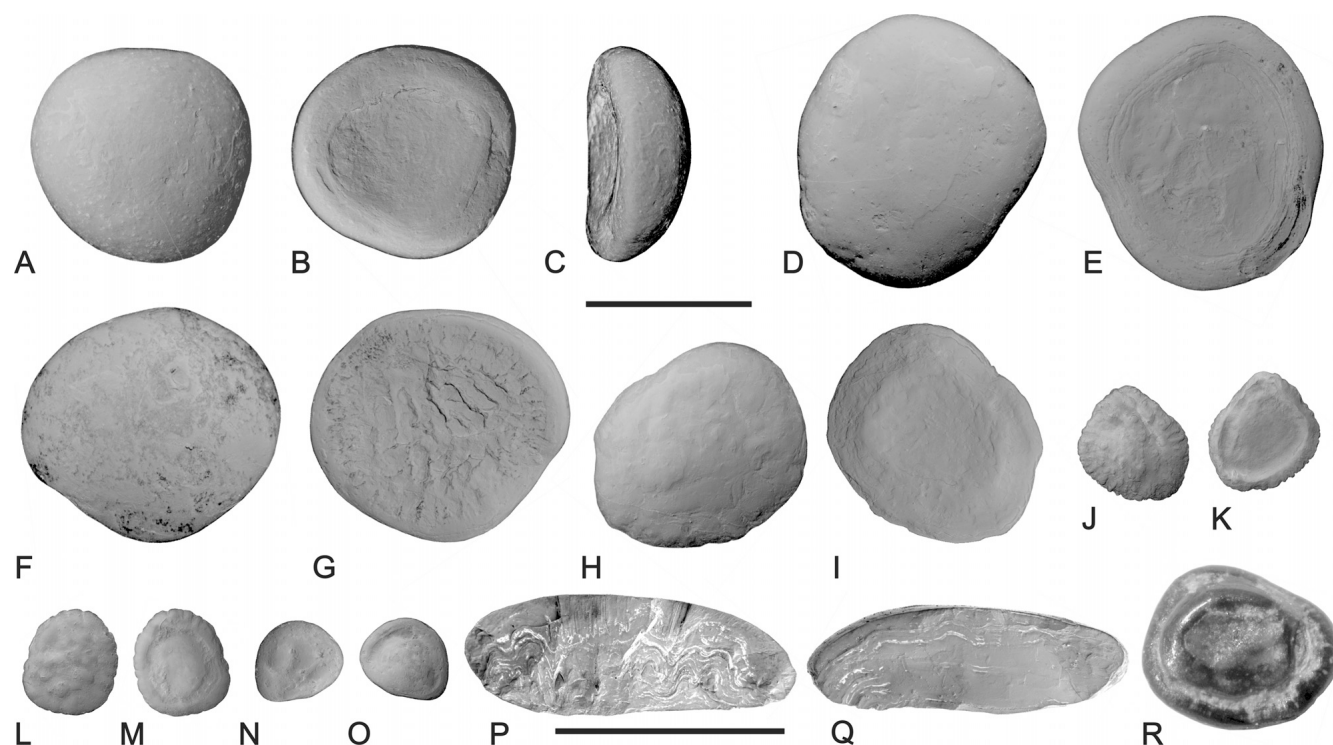


FIGURE 3. Isolated, albuliform teeth from the Wadhurst Clay Formation at Ashdown Brickworks, East Sussex, U.K. **A–C**, BEXHM:2012.21.1 in **A**, occlusal; **B**, basal; and **C**, slightly oblique lateral views. **D**, **E**, BEXHM:2012.21.2 in **D**, occlusal and **E**, basal views. **F**, **G**, BEXHM:2012.21.3 in **F**, occlusal and **G**, basal views. **H**, **I**, BEXHM:2012.21.4 in **H**, occlusal and **I**, basal views. **J**, **K**, BEXHM:20012.21.5 in **J**, occlusal and **K**, basal views. **L**, **M**, BEXHM:2012.21.6 in **L**, occlusal and **M**, basal views. **N**, **O**, BEXHM:2012.21.7 in **N**, occlusal and **O**, basal views. **P**, cross-section of BEXHM:2012.21.8 revealing apparently strongly folded orthodontine in layers of variable thickness and tubules in the (upper) acrodin layer. **Q**, cross-section of BEXHM:2012.21.9 showing orthodontine layers of subequal thickness, only slightly folded, and generally following the (upper) occlusal surface of the tooth. **R**, BEXHM:2012. 21.10 in basal view to show a replacement tooth underlying a functional tooth. **A–Q**, scanning electron micrographs of uncoated specimens (images taken at an acceleration voltage of 1 kV). **R**, photograph in normal light. Scale bars equal 2 mm; the upper applies to **A–O**, the lower to **P–R**.

also represent the first European record from a freshwater deposit. However, as no tooth-bearing bones have yet been recovered, it is not possible to ascertain whether or not the smaller teeth represent those of juveniles or position in the dentition of adults. Similarly, it is not currently possible to determine whether they represent a single species or more than one. Based on currently available material, tooth replacement appears to be of the phyllodontine type, with replacement teeth stacked directly below functional teeth (Estes, 1969), a conclusion supported by the morphology of isolated teeth. If the Ashdown teeth represent a member of the Phyllodontinae, their occurrence requires a partial rejection of Estes' (1969) hypothesis that the Phyllodontinae evolved from a paraboline ancestor, possibly in North America, sometime in the Late Cretaceous. If the Valanginian Ashdown albuliform is a phyllodontine, the taxon would have originated no later than the Early Cretaceous. More complete material from the Valanginian of Britain is required in order to clarify the systematic position of the Ashdown albuliform and shed further light on the evolution and biogeography of the Phyllodontidae.

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